THERMAL ECOLOGY OF BLACK RAT SNAKES (*ELAPHE OBSOLETA*) IN A THERMALLY CHALLENGING ENVIRONMENT

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Abstract. A general model in thermal ecology predicts that ectotherms should stop thermoregulating when the costs outweigh the benefits. Support for this model comes from studies of warm-temperate species, but the extent to which the model can be extrapolated to species living in climatic extremes is unknown, because of the lack of information regarding the thermoregulatory behavior of such species. We tested the applicability of this cost-benefit model using data for black rat snakes (Elaphe obsoleta obsoleta) studied at the northern extreme of their range in Ontario. During 1997-1999, we used automated temperature-sensitive radiotelemetry to collect $\sim 150\,000$ body temperatures from 53 freeranging rat snakes. Simultaneously, we used physical models of snakes to measure the environmental operative temperatures available to black rat snakes, and we determined their preferred body temperature range in a laboratory thermal gradient. The mostly forested habitats inhabited by rat snakes in Ontario were more thermally challenging than the habitats of other species studied to date. The preferred body temperature ranges of male, nongravid female, and gravid female black rat snakes were not significantly different (preferred body temperature averaged across all individuals, 28.1°C). However, free-ranging gravid females tended to maintain higher body temperatures in order to thermoregulate more effectively as well as exploit their thermal environment more than males and nongravid females. This difference was most pronounced during the day and prior to egg laying, and constituted the first documentation of such a phenomenon in an oviparous snake. Black rat snakes had indices of thermoregulation effectiveness similar to other species but tended to exploit opportunities for thermoregulation less. Overall, our data provided support that was at best ambiguous for the current cost-benefit thermoregulation model, suggesting that this model may generally be less applicable to species inhabiting climatic extremes. We propose that, for species in extreme climates, the costs associated with thermoconformity may be more important than previously recognized. We identified several problems associated with the index of thermoregulation effectiveness used by previous researchers, and we propose a mathematically simpler alternative that circumvents these problems. We also make recommendations regarding the future use of the various indices of thermoregulation developed in recent years.

Key words: black rat snake; cost–benefit thermoregulation; ectotherm; Elaphe obsoleta obsoleta; *Ontario, Canada; reptile; thermal challenge; thermal exploitation; thermoconformer; thermoregulation; thermoconformity.*

INTRODUCTION

Some reptiles are precise thermoregulators and are only active under a narrow range of body temperatures (T_b) (Adolph 1990). Other reptiles are thermal conformers and are active under a broader range of T_b (Ruibal and Philibosian 1970, Moore 1978, Hertz 1992). Differences between species in the costs and benefits of thermoregulation are assumed to account for this variation (Huey and Slatkin 1976). The most obvious cost is time, because time spent thermoregulating, or waiting for conditions that allow thermoregulation, is not available for other activities (Huey and Slatkin 1976). The main benefit of thermoregulation is physiological, because most physiological processes occur optimally under a narrow range of $T_{\rm b}$ (Peterson et al. 1993). Under the cost-benefit model, thermoconformity is expected when climatic extremes make precise thermoregulation too expensive (Huey and Slatkin 1976, Withers and Campbell 1985). Although data in support of this prediction have been presented for species that experience relatively benign thermal environments (Lee 1980, Hertz and Huey 1981, Huey 1982), its general validity remains uncertain, largely because the research bias toward studying the thermal ecology of warm-temperate reptiles (Shine and Madsen 1996) has resulted in very few studies being conducted at climatic extremes. Therefore, it is unknown whether the cost-benefit model can be extrapolated to species

Manuscript received 24 August 2000; revised 15 December 2000; accepted 23 December 2000; final version received 23 January 2001.

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experiencing very challenging thermal environments. Furthermore, results of a recent study by Brown and Weatherhead (2000) cast doubt on the validity of the prediction. They found that northern water snakes (*Nerodia sipedon*) were fairly precise thermoregulators even though they studied the species near the northern limit of snake distributions in Canada. Our general goal in this study is to investigate the thermal ecology of black rat snakes (*Elaphe obsoleta obsoleta* (Say)) near the northern limit of their distribution to determine if they are thermoconformers, and thus assess the utility of the cost–benefit model of thermoregulation.

The thermoregulation cost depends on the biophysical environment, which includes factors such as the spatial distribution of operative environmental temperatures (T_e) in the habitat (Withers and Campbell 1985), competition (Labra 1995), and predation risk (Huey 1982). In Brown and Weatherhead's (2000) study, the habitat occupied by northern water snakes (shallow beaver ponds) provided microhabitats with T_{e} within the snakes' preferred range of $T_{\rm b}$ through much of the snakes' active season. Thus, the thermoregulation cost, at least in terms of the availability of appropriate values of $T_{\rm e}$, was low. The consequence of living in an extreme climate for these northern water snakes, therefore, was that temperature restricted the length of their active season (to five months annually), but not their activity within the active season. This is clearly different from the expectation that temperature constraints would result in thermoconformity by the snakes throughout their active season.

The black rat snakes that we studied differ ecologically from Brown and Weatherhead's (2000) northern water snakes in several ways that are relevant to our goal. Although both species in Ontario are near the northern limit of their ranges, and are close to the northern limit of snake distribution in eastern North America (Conant and Collins 1991), and both have brief active seasons, the habitats they occupy are very different. Water snakes occur in open marshes that allow ready access to direct sunlight, and the shallow water provides a thermally optimal microclimate around the clock through much of the active season (Brown and Weatherhead 2000). In contrast, black rat snakes occur in landscapes that are predominantly forested (Blouin-Demers and Weatherhead 2001), which should reduce the availability of microhabitats in which basking is possible. Thus, black rat snakes in this population should be more thermally constrained during their active season, relative to northern water snakes.

Our first specific objective was to quantify the thermal quality (from an ectotherm's perspective) of the black rat snake's environment by assessing the quality of the different habitats available to them. The thermal quality of a habitat has been defined as the extent to which the habitat allows an ectotherm to achieve body temperatures within their preferred T_b range (Hertz et al. 1993). Our second objective was to determine the extent to which black rat snakes take advantage of the available opportunities to maintain T_b within their preferred range, or, conversely, the extent to which they are thermoconformers. We used several indices of thermoregulation to quantify the thermal quality of the snakes' environment and the thermoregulatory behavior of the snakes (Hertz et al. 1993, Christian and Weavers 1996, Brown and Weatherhead 2000). Although all these indices provide different insights, their proliferation has made the quantification of thermal ecology somewhat cumbersome. Therefore, a secondary objective of this paper is to examine critically the usefulness of all the thermoregulation indices proposed in recent years and make recommendations regarding their future use.

In addition to the relevance of this paper to understanding the thermal ecology of reptiles in general, we also use our observations to provide insight into the thermoregulatory behavior of oviparous snakes. Reproduction can influence thermoregulation and habitat use by females. Gravid females of many viviparous species thermoregulate differently from nongravid females and males (e.g., Charland and Gregory 1990, Brown and Weatherhead 2000), and the difference in thermal preference appears to be associated with altered habitat preferences (Reinert 1984, Reinert and Zappalorti 1988). Shine and Madsen (1996) suggested that oviparous snake species should behave similarly, but thus far such behavior has not been formally documented. Blouin-Demers and Weatherhead (2001) showed that gravid female black rat snakes (an oviparous species) had a stronger preference for habitat edges relative to nongravid females and males and proposed that this was a function of their higher thermoregulatory needs. Our final objective is to test the prediction that the thermoregulatory behavior of gravid female black rat snakes differs from that of nongravid females and males. This difference should be most pronounced early in the season when females are actually carrying eggs (until the first two weeks of July).

METHODS

Study area and study species

We conducted this study during 1997–1999 in a 10 \times 3 km study area at the Queen's University Biological Station (QUBS). The study site is close to the geographic center of the Frontenac Axis population of black rat snakes in eastern Ontario and northern New York State (Blouin-Demers et al. 2000*a*: Fig. 1). The habitat in the study area was predominantly mature second-growth deciduous forest. Lakes, other wetlands, and rock outcrops provided natural gaps and edge habitats in the forest. Artificial gaps and edges were created by small hay fields and several secondary dirt roads (Blouin-Demers and Weatherhead 2001).

Radiotelemetry

We captured the majority of snakes for telemetry during spring emergence by building fences fitted with funnel traps around communal hibernacula (Blouin-Demers et al. 2000a). We also used some snakes captured opportunistically during fieldwork during the active season (Prior et al. 2001). All snakes were sexed by probing the cloaca for the presence of hemipenes with a lubricated cloacal probe, measured for snout-vent length (SVL) to the nearest millimeter with a flexible measuring tape, and weighed to the nearest gram with a calibrated spring scale. Snakes selected to be implanted with temperature-sensitive radio transmitters (Model SI-2T, Holohil Systems, Carp, Ontario, Canada; 8.6 g, 20 mo battery life at 20°C) had to be large enough to bear the transmitter (maximum ratio of transmitter mass: body mass = 0.025:1). Because females reproduce every second or third year on average (G. Blouin-Demers, unpublished data), we implanted more females than males to obtain an adequate sample of gravid females. We used isoflurane delivered via a precision vaporizer to anesthetize the snakes and then sterile surgical techniques to implant the radio transmitters in the body cavity and the antennae just underneath the epidermis. The surgical technique was a modification of the procedure described by Reinert and Cundall (1982). Details of the anesthesia procedures are provided by Blouin-Demers et al. (2000b).

After releasing snakes at their point of capture, we located the snakes on average every 48 h from the snakes' emergence in late April to early May until they reentered their hibernacula in late September to early October. During hibernation, we checked the snakes approximately every three weeks to determine their $T_{\rm b}$ from the pulse rate of the transmitter. For the purpose of this study, we considered the active season of black rat snakes to be 1 May-30 September, based on the average date of 6 May for 801 exits from hibernation by 551 individuals (Blouin-Demers et al. 2000a), and on the average date of 4 October for 59 entries into hibernation by 41 radio-implanted snakes recorded during the present study. During May 1997-November 1999, we followed 17 males and 36 females for periods ranging from 1 to 30 mo (mean, 13.1 ± 1.1 mo). Because females do not reproduce every year, eight females were followed both when they were gravid and nongravid. Thus, we have data from 25 individual females when nongravid and from 19 individual females when gravid. Twenty-three snakes (nine males and 14 females) were followed in multiple years, and we therefore have data for 79 "snake years" (25 "male years," 33 "nongravid female years," and 21 "gravid female years").

The radio transmitters we used had pulse rates proportional to temperature. Calibration curves were supplied by the manufacturer for each transmitter (pulse rates ranging $0-40^{\circ}$ C in 5°C increments). Because our own calibrations using a water bath and a mercury thermometer were always within 0.5°C of the manufacturer's, we used the latter calibrations in our calculations. When removing radio transmitters for battery replacement, we determined whether any drift had occurred in the calibration curve. No significant drift (i.e., a shift of $\geq 0.5^{\circ}$ C in estimated temperature at a given pulse rate) was ever recorded. We used polynomial regressions (including all terms up to degree four) and the eight calibration points for each radio transmitter to derive an equation to predict temperature based on pulse rate. All calibration equations provided a very high degree of fit ($R^2 \geq 0.9999$ in all instances).

We obtained $T_{\rm b}$ values of black rat snakes "manually" and using automated receivers. Values were obtained manually each time we located a snake (every 48 h during the active season, every three weeks during hibernation). We determined the pulse rate of the transmitter with a stopwatch and then used the calibration equation of the transmitter to determine the $T_{\rm b}$ of the individual. Each year we also used two automated radiotelemetry data loggers (SRX 400, Lotek Engineering, Newmarket, Ontario, Canada) to record daily $T_{\rm b}$ profiles of black rat snakes from the emergence of the first radio-implanted individual (April) to the entry into hibernation of the last individual (October). We entered all the calibration equations in both loggers and then programmed the loggers to scan the frequency of each radio transmitter every 10 min. Each time a snake was within transmission range (the signal of the radio transmitter was clearly distinguished against the background electrostatic noise), the loggers calculated the pulse rate as the mean duration of three pulse intervals, computed the corresponding temperature from the calibration equation of that transmitter, and stored the date, time, transmitter frequency, and temperature. Because black rat snakes are wide ranging and the transmission range was limited to \sim 500 m, depending on the snake's position, we could not obtain complete $T_{\rm b}$ profiles for all individuals. However, we regularly moved the two loggers to maximize the number of snakes that were within transmission range at any given time.

Thermal preference

In our analyses of thermoregulation we use the terminology and symbols introduced by Hertz et al. (1993) and subsequently followed by most researchers. The first step in studying thermoregulation is to determine the range of preferred body temperatures $(T_{\rm set})$ of the study species. This set of preferred temperatures should be measured in an environment where there are no thermoregulatory costs (Huey and Slatkin 1976, Hertz et al. 1993). Hence, we measured T_{set} using a thermal gradient chamber in the laboratory. The chamber was a plywood box ($250 \times 60 \times 60$ cm) with a fluorescent light that provided constant and homogeneous illumination. A coil of tubing through which cold water was constantly circulating under one end of the chamber, and a heating pad at the other end of the chamber, produced a smooth gradient ranging from 15° to 40°C. We introduced postabsorptive (fasted for seven days), radio-implanted rat snakes individually in the chamber and gave them 24 h to acclimatize to the setting. Then we recorded the $T_{\rm b}$ they selected in the gradient every 10 min for 24 h using one of the telemetry data loggers. We used the bounds of the central 50% of observed range of $T_{\rm b}$ for each individual to determine $T_{\rm set}$ (Hertz et al. 1993, Christian and Weavers 1996).

Operative environmental temperatures

The possible values of $T_{\rm b}$ available to an ectotherm in the field are referred to as the operative environmental temperatures ($T_{\rm e}$). Operative environmental temperatures can be determined using complex mathematical models that integrate all the heat exchange parameters to predict $T_{\rm b}$ for a given species under a fixed set of environmental conditions (Scott et al. 1982, Bakken 1992). A simpler approach for determining $T_{\rm e}$ is to install in the field a series of physical models that have the same thermal characteristics as the species of interest. These physical models are used as " $T_{\rm e}$ thermometers" and allow one to quantify over time and space the $T_{\rm b}$ range the study animal could potentially achieve in the field. We used a combination of these two approaches in the present study.

We constructed two models of black rat snakes using copper pipes. The models were 40 cm long and had a diameter of 4 cm. We painted the models with glossy black metal paint to approximate the reflectance of black rat snakes (Peterson et al. 1993). We suspended a thermocouple in the center of each model with stiff metal wire, filled the models with water, and then sealed both ends of each model with a plastic cap and silicone. We calibrated the models using two fresh carcasses of rat snakes found dead on the road. The carcasses were at each extreme of the range of masses of snakes with transmitters: the mass of one was 400 g, and the other was 1200 g. We placed the two carcasses beside one of the copper models on bare ground on three sunny days in August 1998 and recorded the temperatures in the carcasses and the model every 10 min from dawn to dusk using one of the data loggers and a radio transmitter placed in each carcass and in the model.

To record environmental operative temperatures, we placed one model on bare ground in the open and permanently connected its thermocouple to the meteorological station at QUBS. The station recorded the temperature of the model, air temperature 1.5 m aboveground in a Stevenson screen, wind speed at 5 m aboveground, and solar radiation at 2 m aboveground every minute and evaluated the means of all the data for each hour. The thermocouple of the other model was connected to a miniature temperature data logger (HOBO Temp, ONSET Computer Corporation, Pocasset, Massachusetts, USA) that recorded the model's internal temperature every 10 min, which we then averaged for each hour. We alternately placed this second model in a minimum of four and a maximum of eight locations in a given habitat for a total duration of three to six weeks and then moved it to another habitat. The principal habitats in the study area are forest, rock outcrop, field, wetland, and open water (Blouin-Demers and Weatherhead 2001). We measured $T_{\rm e}$ readings by placing the model snake in forest, hay fields, and in rock outcrops. Because black rat snakes are terrestrial (Blouin-Demers and Weatherhead 2001), we did not measure T_e in water. Rat snakes are sometimes found near the edges of wetlands (primarily marshes with sedges, Carex, and cattails, Thypha). However, because these wetlands are structurally similar to fields, we considered the T_{e} for wetlands to be the same as for fields. When positioning the model in the different habitats, we were sensitive to the natural history of black rat snakes and selected microhabitats that were accessible to the snakes. We always placed the model on the ground, except in forests where we also placed the model on tree branches. Finally, there were a number of retreat sites (rock piles, crevices in rock outcrops, large logs, old barns, old machinery, inside snags) buffered from outside variation in microclimate that were used by all snakes and that could not be adequately classified in any of the above categories. Therefore, we also placed the portable model in two representative retreat sites (under flat rocks on rock outcrops and in barns) to measure $T_{\rm e}$ available to black rat snakes in such retreats.

We concede that we did not attempt to capture every nuance of microhabitat variability with our $T_{\rm e}$ -sampling protocol, but rather we wanted to establish the general thermal properties of each habitat. However, thermal heterogeneity was much less within a habitat than among habitats. For example, deriving separate $T_{\rm e}$ predictive equations for each habitat based on the different model locations produced very small mean ($\sim 1^{\circ}$ C) and maximum ($\sim 3^{\circ}$ C) T_{e} estimation differences (in absolute values). Also, our methods to quantify $T_{\rm e}$ were more detailed than methods employed by many previous researchers. For example, Christian et al. (1983), Christian and Bedford (1995), and Christian and Weavers (1996) only measured $T_{\rm e}$ in the two most extreme habitats (full sun and full shade) and assumed that, by shuttling and selecting sites of partial shade, their study animals could achieve any value of $T_{\rm e}$ in between the two extremes. Although not exhaustively quantifying thermal heterogeneity within habitats (which may be important for species whose movements are small in relation to the spatial interspersion of the habitats) does decrease the resolution of $T_{\rm e}$ as originally proposed by Hertz et al. (1993), $T_{\rm e}$ calculated in this fashion nevertheless does serve as an index of available environmental operative temperatures.

To determine T_e available in all habitats at all times, we derived multiple regression equations to predict model temperature in a given habitat based on the four microclimatic variables recorded by the weather station. We used the MAXR procedure of SAS (SAS Institute 1990) to find the combination of climatic variables that best predicted model temperature (maxiNovember 2001

mized the R^2) in each of the habitats. For four variables, the MAXR procedure finds the best model using one, two, three, or four variables. Among these four models for each habitat, we chose the one that included the most significant variables based on their Type III sum of squares because we had no a priori reason to favor a particular ordering of the variables. We used the equation of each of the selected models to generate T_e values for each habitat for the duration of the study. To obtain a measure of the average operative temperature of the habitat available to black rat snakes, we calculated a mean of the T_e measurements of all the habitats for each hour. This method of calculating mean T_e assumes that each snake was aware of and had access to all habitats in the study area. This assumption seems reasonable because (1) black rat snakes can travel very long distances in a short time period (e.g. ~5000 m

habitats in the study area. This assumption seems reasonable because (1) black rat snakes can travel very long distances in a short time period (e.g., ~5000 m in two days; G. Blouin-Demers, *unpublished data*), (2) the habitat patches in the study area are interspersed and small in comparison to the size of the snakes' home ranges (Weatherhead and Charland 1985, Weatherhead and Hoysak 1989), (3) black rat snakes are not territorial and have broadly overlapping home ranges and should thus be free to choose the best available habitat (Weatherhead and Hoysak 1989), and (4) abundant evidence of behavioral thermoregulation for various species indicates that ectotherms are aware of their thermal options.

Extent of thermoregulation

Thermoregulation indices developed in recent years compare the extent to which a study animal actually experiences a body temperature (T_b) within its preferred range of body temperatures (T_{set}) (the "accuracy" of $T_{\rm b}$) to the extent to which the habitat in which it lives allows $T_{\rm b}$ within the $T_{\rm set}$ to be reached (the thermal quality of the habitat). Following Hertz et al. (1993), we measured the accuracy of $T_{\rm b}$ as the mean of the deviations of $T_{\rm b}$ from $T_{\rm set}$ (individual deviation, $d_{\rm b}$). If $T_{\rm b}$ is below the preferred range, then $d_{\rm b}$ is the difference between the lower bound of T_{set} and T_b , and if T_b is above T_{set} , d_{b} is the difference between T_{b} and the upper bound of T_{set} . Similarly, we measured the thermal quality of each habitat by the mean of the deviations of $T_{\rm e}$ from T_{set} (individual deviation, d_{e}) in each habitat. If $T_{\rm e}$ is below the set point range, $d_{\rm e}$ is the difference between the lower bound of T_{set} and T_e , and if T_e is above T_{set} , d_{e} is the difference between T_{e} and the upper bound of T_{set} .

Elsewhere, we showed that black rat snakes preferentially use the edges between forest and open habitats such as rock outcrops or fields (Blouin-Demers and Weatherhead 2001). We defined edges as the habitat within 15 m of the boundary between forest and any open habitat, and evaluated the thermal quality of edges by assuming that snakes in a habitat edge had access to the habitats on either side of the edge at virtually no cost. Because T_e values exceeded the upper bound of T_{set} in only 1.5% of the observations in the forest (see Results), we considered that forested habitats always provided a refuge from high temperatures. Therefore, to calculate $d_{\rm e}$ in edge habitats, we were only interested in instances where the lower bound of $T_{\rm set}$ could not be reached in the forested or open habitat, because, even when $T_{\rm e}$ exceeded the upper bound of $T_{\rm set}$ in the open habitat, snakes could use the forested habitat to cool down. Hence, we assigned d_e a value greater than zero only when $T_{\rm e}$ in both habitats was less than the lower bound of T_{set} . We defined d_e in edges as the minimum deviation from the lower bound of T_{set} in the forested or in the open habitats. Using this method, we calculated d_{e} values for the edge between forest and rock outcrop and the edge between forest and field/ wetland. To calculate d_e for the edge between forest and water bodies, we employed this method using T_{e} measurements for the model snake on open bare ground, because the shorelines of open water in the study area usually included bare ground.

From measures of the accuracy of $T_{\rm b}$ (= $d_{\rm b}$) and of the thermal quality of habitats (= $d_{\rm e}$), Hertz et al. (1993) derived an index of the effectiveness of thermoregulation (E), which they used to compare the thermoregulatory behavior of different populations or species. Brown and Weatherhead (2000) used this index to compare the thermoregulatory behavior of different segments or different individuals within a population, and we follow their approach here. The index of effectiveness of thermoregulation is calculated as E = 1 $-(\bar{d}_{\rm b}/\bar{d}_{\rm e})$, where the overbars indicate mean values of the deviations. When animals do not thermoregulate and select microhabitats randomly with respect to T_{e} , $d_{\rm b}$ and $d_{\rm e}$ will be similar, and E will tend toward zero. However, if animals thermoregulate carefully, $d_{\rm b}$ will be much smaller than d_e and E will tend toward a value of one. Negative values of E indicate that animals actually avoid habitats with T_{e} within the range T_{set} . When calculating E, we evaluated the mean value of d_{e} for all habitats each hour to obtain a measure of the average thermal quality of the habitat available to black rat snakes.

An additional index of thermoregulation (E_x) that determines the extent to which animals exploit the thermal environment was developed by Christian and Weavers (1996). E_x is defined as the amount of time an animal spends within its $T_{\rm set}$, expressed as a percentage of the time that it was possible for the animal to do so (as indicated by the $T_{\rm e}$ data). Therefore, we calculated E_x as the proportion of T_b measurements that fell within T_{set} for times when $d_e = 0$ in at least one of the habitats. Following Brown and Weatherhead (2000), we also modified this index slightly to calculate the proportions of $T_{\rm b}$ measurements that fell below and above T_{set} when the $d_{\text{e}} = 0$ in at least one of the habitats. We used these different indices of thermoregulation in this study because the question of how carefully an ectotherm regulates its body temparature is actually a

TABLE 1. Mean body temperatures (T_{b} , in °C) selected, 75% quartile, and 25% quartile (means \pm 1 sE), with range appearing in parentheses) for male, nongravid female, and gravid female black rat snakes from Ontario (Canada) in a laboratory thermal gradient.

Group	Ν	Mean T _b	75% quartile	25% quartile
Males	9	27.4 ± 0.94	29.6 ± 0.99	25.5 ± 1.05
		(25.0 - 30.7)	(27.6 - 32.2)	(22.3 - 29.5)
Nongravid females	21	28.3 ± 0.62	29.9 ± 0.65	26.8 ± 0.69
		(22.5 - 31.7)	(23.5 - 33.4)	(21.5 - 31.0)
Gravid females	11	28.2 ± 0.85	30.0 ± 0.90	26.6 ± 0.95
		(19.5 - 32.8)	(20.9 - 33.7)	(18.0 - 32.3)

suite of questions that require different methods to answer (Hertz et al. 1993). For example, d_b was designed to quantify the "accuracy" of T_b (i.e., how much T_b data points deviate from T_{set} on average), and similarly d_e quantifies the thermal quality of a habitat by providing a measure of how much T_e values deviate from T_{set} on average. *E* quantifies how much departure there is from perfect thermoconformity (i.e., $d_e = d_b$), and E_x measures the extent to which ectotherms exploit the available opportunities for thermoregulation, but ignores the behavior of the animal when a value of T_e within T_{set} is not available.

Statistical analyses

We separately analyzed data for males, nongravid females, and gravid females. The reproductive state of females was assessed in June by externally palpating the oviducts for the presence of eggs and confirmed in July by nesting activity. Series of $T_{\rm b}$ values recorded from a single individual are not independent. Therefore, all analyses were performed on data $(T_b, E, \text{ or } E_x)$ averaged for each individual over the period appropriate for the specific analysis (year, month, hour), thereby avoiding pseudoreplication (Shine and Madsen 1996, Stevens 1996). Some females changed reproductive status from one year to the next (gravid vs. nongravid). Thus, we considered body temperature measured for an individual in different years independent. For most individual snakes, we did not have complete $T_{\rm b}$ data for three main reasons: (1) snakes regularly moved out of the data loggers' range, (2) some snakes were killed by predators before the termination of the study, and (3) radio transmitters failed unexpectedly. Therefore, it was not practical to use repeated-measure analyses on individuals to analyze our data.

The analyses were conducted on JMP Version 3.2 (SAS Institute 1997), SPSS Version 6.1 (SPSS 1995), and a mainframe version of SAS (SAS Institute 1990) on a Macintosh desktop computer. We inspected box plots to determine if the assumptions of normality and homogeneity of variance were upheld. We detected no significant violations of these assumptions. Significance of statistical tests was accepted at $\alpha = 0.05$, but marginally nonsignificant results are discussed when deemed important. All means are reported ± 1 sE unless otherwise stated.

Results

During April 1997–November 1999, we recorded 150 368 body temperature (T_b) measurements from the 53 individuals (17 males, 36 females). Of these, 3786 (2.5%) were recorded manually, and the remaining 146 582 (97.5%) were recorded on the automated data loggers. We reduced these observations to 34 211 hourly mean T_b values that we used as the basis for all analyses. Of these hourly mean T_b data points, 29 722 (86.9%) were from the active season (1 May–30 September), and 4489 (13.1%) were from the hibernation period. Of the T_b values recorded during the active season, 17 086 (57.5%) were recorded during the day (0600–1800) and the remaining 12 636 (42.5%) during the night.

Thermal preference

In total, nine males, 21 nongravid females, and 11 gravid females were placed in the thermal gradient. For six females, we measured the range of preferred body temperatures (T_{set}) both when they were gravid and when they were not gravid. For each individual, we calculated the mean $T_{\rm b}$ in the gradient and the 75% and 25% quartiles (Hertz et al. 1993). Averaged across all individuals, the mean $T_{\rm b}$ selected in the thermal gradient was 28.1°C and the mean 75% and 25% quartiles were 29.8°C and 26.5°C, respectively (Table 1). Oneway ANOVAs revealed no significant differences among males, nongravid females, and gravid females for any of these parameters (mean $T_{\rm b}$, $F_{2,38} = 0.288$, P = 0.75; 75% quartile, $F_{2,38}$ = 0.050, P = 0.95; 25% quartile, $F_{2,38} = 0.523$, P = 0.60). For the six females tested both when gravid and nongravid, we contrasted the three thermal selection parameters using paired ttests. For each parameter, there was no significant difference between reproductive states (mean $T_{\rm b}$, paired $t_5 = 0.012, P = 0.99; 75\%$ quartile, paired $t_5 = 0.030,$ P = 0.98; 25% quartile, paired $t_5 = -0.162$, P = 0.88).

To determine whether the snakes preferred the same temperatures in the field as in the laboratory when conditions in the field allowed, we calculated the mean T_b during the active season in the field for each individual and its 75% and 25% quartiles. We restricted these calculations to periods when the operative environmental temperatures (T_e) in the different habitats available to black rat snakes indicated that the lower bound

			Significance		
Habitat	Equation	R^2	F	df	Р
Forest Field/wetland Rock outcrop Bare ground in open Barn Under flat rock	$\begin{array}{r} 1.16T + 0.66R - 0.02W - 4.07 \\ 1.25T + 31.12R - 9.44 \\ 1.42T + 24.39R + 0.18W - 7.60 \\ 1.26T + 28.63R - 0.08W - 5.83 \\ 0.77T - 0.50R + 0.48RA + 6.19 \\ 1.06T - 11.36R + 0.06W + 3.68 \end{array}$	0.86 0.94 0.89 0.94 0.56 0.92	1567.15 4337.20 1882.68 5083.90 347.92 1126.70	3, 764 2, 587 3, 717 3, 1002 3, 817 3, 284	$\begin{array}{c} 0.0001 \\ 0.0001 \\ 0.0001 \\ 0.0001 \\ 0.0001 \\ 0.0001 \\ 0.0001 \end{array}$

TABLE 2. Multiple regression equations used to predict model snake temperature in the different habitats available to black rat snakes in Ontario, and their statistical significance.

Notes: The snake models were positioned in four to eight locations in each different habitat. The variables entered as predictors in the models were air temperature (T) in °C, solar radiation (R) in kW/m², wind speed (W) in m/s, and rainfall (RA) in mm/h.

of T_{set} (26.5°C) could have been reached in at least one habitat (see *Results: Thermal exploitation*). Averaged across all individuals, the mean T_b in the field during periods when it was possible to have T_b values within T_{set} was 25.2°C, and the mean 75% and 25% quartiles were 28.7°C and 22.1°C, respectively. Therefore, even when conditions in the field allowed black rat snakes to attain body temperatures in their preferred range, their mean T_b values, 75% quartiles, and 25% quartiles were lower than those selected in the laboratory thermal gradient (28.1°C, 29.8°C, and 26.5°C, respectively). Differences between these laboratory and field temperatures were significant (*t* tests, $t_{90} > 2.53$ and P <0.01 in all cases).

Operative environmental temperatures

The temperatures of the 1200-g snake carcass and the copper snake model were highly correlated (r =0.98, $F_{1,100} = 1800.3$, P < 0.001) and the mean temperatures of the carcass and of the model were not significantly different (mean difference, $-0.17 \pm$ 0.16°C, paired $t_{101} = -1.07$, P = 0.285). The temperature of the 400-g carcass was also highly correlated with the temperature of the snake model (r = 0.98, $F_{1.80}$ = 2837.4, P < 0.001), but the difference between the mean temperatures of the 400-g carcass and of the model was significant (mean difference, $-0.51 \pm 0.12^{\circ}$ C, paired $t_{81} = -4.22$, P < 0.001) and indicated that the model tended to slightly overestimate the carcass temperature. However, because the mean difference between the model and carcass temperatures was very small and approximately the same as the transmitter calibration error (our calibrations vs. the manufacturer's), it is not biologically meaningful. Thus, we assumed the snake models accurately measured the available $T_{\rm b}$ for the size range of black rat snakes we were monitoring.

We derived multiple regression equations to predict model snake temperatures in each habitat based on the four microclimatic variables. The maximum simple correlation (r) between pairs of variables used in the analysis was 0.47, and the highest variance inflation factor for any of the equation terms was 2.5. All equations were highly significant and explained a large proportion of the total variance (mean $R^2 = 0.85$, range in R^2 , 0.56–0.94; Table 2). We used these equations to calculate hourly T_e values for 1 May–30 September of each year for the different habitats.

Thermal quality of habitats

We calculated monthly mean $T_{\rm e}$ values based on all mean hourly T_e data measured during the active season over the three years. Mean T_{e} increased from the lowest point in May to a peak in July and then decreased in August and September, but mean $T_{\rm e}$ never exceeded the lower bound of T_{set} in any month (Fig. 1), indicating that the habitat of black rat snakes in Ontario is thermally challenging. Forests had the lowest mean T_{e} (Table 3) and were the coolest habitat for most of the day (Fig. 1). In fact, T_{e} exceeded the upper limit of T_{set} (29.8°C) in only 166 of 10719 observations (1.5%) in the forest. Therefore, we considered that forests offered rat snakes a permanent refuge from high temperatures. We used the mean d_e calculated for the entire active season to measure the average thermal quality of the habitats available to black rat snakes. Mean d_{e} values varied from 5.5° to 12.0°C for the different habitats. Mean $d_{\rm e}$ was highest for the open habitats (field/wetlands, bare ground, and rock outcrops), intermediate for forests, and lowest for the two retreat sites (barns and under rocks) and for the three types of edges (Table 3).

Body temperatures $(T_{\rm b})$

We calculated mean monthly body temperatures for each individual in each year based on the hourly mean $T_{\rm b}$ measurements, and then averaged these individual means for each month of the year. Mean monthly $T_{\rm b}$ was at a minimum toward the end of hibernation in March (5.6°C), increased at the start of the active season to reach a peak in June (24.2°C) and July (25.4°C), and then gradually decreased from August to March (Fig. 2). The distribution of mean hourly $T_{\rm b}$ and $T_{\rm e}$ during the active season indicated that black rat snakes avoided temperature extremes and selected habitats that allowed them to maintain $T_{\rm b}$ values above the mean $T_{\rm e}$ (Fig. 3). Body temperatures were within $T_{\rm set}$ 17.5% of



FIG. 1. (A) Mean operative environmental temperatures $(T_e \pm 1 \text{ sE})$ for each month of the active season, and (B) mean operative environmental temperatures for each hour of the day under flat rocks (filled circles), inside barns (filled triangles), on rock outcrops (open circles), in forests (open triangles), on bare ground in the open (open squares), and in fields (open lozenges) in Ontario. The range of preferred body temperatures (T_{set}) for black rat snakes in Ontario is represented by the horizontal solid lines.

the time, whereas mean $T_{\rm e}$ for all the habitats fell within $T_{\rm set}$ only 8.3% of the time.

We averaged hourly $T_{\rm b}$ measurements for each individual for each hour of the day in each year. We similarly calculated mean maximum $T_{\rm e}$ and mean minimum $T_{\rm e}$ for each hour. A plot of mean $T_{\rm b}$, mean maximum $T_{\rm e}$, and mean minimum $T_{\rm e}$ through the day revealed that black rat snakes were as warm as their environment allowed at night between ~2200 and 0600, but that the snakes did not fully use opportunities to reach body temperatures within the bounds of $T_{\rm set}$ during the day (Fig. 4). When we considered the whole active season, the mean hourly $T_{\rm b}$ values of black rat TABLE 3. Mean \pm 1 SE operative temperatures (T_e) recorded in each habitat available to black rat snakes in Ontario and mean \pm 1 SE deviations (d_e) of operative temperatures from the preferred body temperature range of black rat snakes in each habitat.

Habitat	Mean T _e	Mean d_{e}
Forest Field/wetland Rock outcrop Bare ground in open Barn Under flat rock	$17.5 \pm 0.0620.8 \pm 0.1325.9 \pm 0.1323.3 \pm 0.1220.4 \pm 0.0421.5 \pm 0.05$	$\begin{array}{c} 9.2 \pm 0.06 \\ 12.0 \pm 0.07 \\ 9.5 \pm 0.07 \\ 10.3 \pm 0.06 \\ 6.2 \pm 0.04 \\ 5.5 \pm 0.04 \end{array}$
Edge forest-field/wetland Edge forest-rock outcrop Edge forest-water body		$\begin{array}{l} 7.5 \ \pm \ 0.06 \\ 5.6 \ \pm \ 0.06 \\ 7.0 \ \pm \ 0.06 \end{array}$

snakes never reached the lower bound of T_{set} during the day, although it would have been possible to have T_{b} within T_{set} between ~0800 and 1900 daily. Thus, black rat snakes appeared to exploit their thermal environment maximally at night but not during the day. Even if we only consider the warmest month (July), on average black rat snakes maintained T_{b} within T_{set} from 1100 to 1800 even though values of T_{e} indicated that it would have been possible to have T_{b} within T_{set} from 0700 to 2100 (Fig. 4).

We also used the mean monthly T_b data for each individual in each year to determine if body temperature differed between the three sex/reproductive groups, and whether any differences varied seasonally. We used mean T_b as the response variable in a twoway ANCOVA where mean monthly T_e , sex/reproductive group, month, and the interaction between group and month were entered as predictor variables. We entered mean monthly T_e as a factor in the analysis to control for the potential effect of measuring T_b on different individuals under different climatic conditions. We conducted the same analysis separately for day



FIG. 2. Mean body temperatures ($T_{\rm b} \pm 1$ SE) maintained by black rat snakes in Ontario for each month of the years 1997–1999.



FIG. 3. (A) Frequency distribution of hourly mean operative environmental temperatures (T_e) , and (B) hourly mean body temperatures (T_b) of black rat snakes in Ontario. The shaded area represents the range of preferred body temperatures (T_{set}) of black rat snakes in Ontario.

(0600–1800) and night (1800–0600). Not surprisingly, mean monthly T_e had a significant effect on the T_b maintained by the snakes. The interaction term was not significant for both day and night, but the effect of reproductive group was significant during the day and nonsignificant at night (Table 4). Tukey-Kramer honestly significant difference (hsd) tests indicated that during the day gravid females maintained significantly higher T_b levels than males and nongravid females, but that males and nongravid females were not significantly different from one another (Fig. 5).

Effectiveness of thermoregulation

We calculated a mean d_b for each individual in each year and then calculated the effectiveness of thermoregulation (*E*) for each individual in each year using the average mean d_e for all the habitats in that year. The mean d_b based on all the individual values was $4.79 \pm 0.22^{\circ}$ C, and the average of the mean d_e for the three years of the study was $8.09 \pm 0.12^{\circ}$ C. The overall average of the individual values of *E* was 0.409 ± 0.025 . Thus, black rat snakes can be referred to as moderately precise thermoregulators given that *E* would equal one if snakes always maintained T_b within T_{set} (pure thermoregulation) and would equal zero if T_b were always as far from T_{set} as T_e (pure thermoconformity).

We used the mean monthly d_b values for each individual in each year to calculate overall mean monthly d_b . Similarly, we averaged the mean monthly d_e values



FIG. 4. Hourly mean body temperatures ($T_{\rm b}$; circles) of black rat snakes in Ontario and hourly mean maximum and minimum operative environmental temperatures ($T_{\rm e}$; lozenges) (A) for the whole season and (B) for July only. The range of preferred body temperatures ($T_{\rm sel}$) for black rat snakes in Ontario is represented by the horizontal solid lines.

TABLE 4. Summary results of the two-way ANCOVAs for the effects of mean monthly operative temperature (T_e) , month, and reproductive group on mean body temperatures of black rat snakes in Ontario for the daytime and nighttime.

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FIG. 5. (A) Mean body temperatures ($T_{\rm b} \pm 1$ SE) and (B) mean index of thermoregulation effectiveness ($E \pm 1$ SE) for the day and night maintained by male (filled bars), nongravid female (hatched bars), and gravid female (open bars) black rat snakes in Ontario. Means with the same letters are deemed not significantly different based on Tukey-Kramer hsd tests.

in each year to obtain overall mean monthly d_{e} . Plotting overall mean $d_{\rm b}$ and overall mean $d_{\rm e}$ as a function of month indicated these two variable followed a similar pattern. Mean $d_{\rm b}$ and mean $d_{\rm e}$ values were highest during May, which was the coldest month, decreased to reach their lowest point in July, which was the warmest month, and then increased again in August and September (Fig. 6). Mean d_e was always higher than mean $d_{\rm b}$, but the difference between $d_{\rm b}$ and $d_{\rm e}$ was highest in July and lowest in September (Fig. 6). We calculated E for each individual in each month of each year using the mean monthly $d_{\rm b}$ of the individual and the mean monthly d_e for that month that year. We then averaged all the individual values of E for each month of the active season. As expected from the previous analysis of the seasonal variation in $d_{\rm b}$ and $d_{\rm e}$, E increased in May and June to reach its highest point (0.55) in July and then decreased to its lowest point in September (0.10) (Fig. 7).

To see how thermoregulation varied during the

course of the day, we also calculated mean hourly d_b for each individual in each year and then took the mean of these values for each hour. We similarly averaged mean hourly d_e values for each year and then averaged d_e for each hour. Overall, mean d_e was higher than mean d_b during the course of the day, except from ~0800–1000 where d_e was actually lower than mean d_b . The difference between d_e and d_b was greatest at night between ~2000–0600 (Fig. 6) when the snakes remained as warm as their environment allowed. We calculated mean hourly E values for each individual in each year and then averaged the individual values for each hour. As expected based on the relative fluctuations of d_b and d_e , E was highest at night (~0.50) from ~2000–0700, was actually negative from ~0800–1000, and was



FIG. 6. Mean deviations of body temperatures from the range of preferred body temperatures ($d_b \pm 1$ sE; open circles) of black rat snakes in Ontario and mean deviations of operative environmental temperatures from the range of preferred body temperatures ($d_e \pm 1$ sE; filled circles) (A) for each month of the active season and (B) for each hour of the day.



FIG. 7. Mean index of thermoregulation effectiveness ($E \pm 1$ sE) of black rat snakes in Ontario (A) for each month of the active season and (B) for each hour of the day.

~0.25 for the rest of the day (Fig. 7). This pattern is a consequence of black rat snakes selecting the warmest available microhabitats at night (presumably retreat sites), thus producing high values of *E*. The snakes then tended to delay their emergence from their nocturnal retreat until approximately three hours after the pronounced morning increase in mean T_e , thus producing negative values of *E* in the early morning. Throughout the remainder of the day, T_b of rat snakes were closer to T_{set} than were mean T_e values, but the snakes did not fully exploit the opportunities to increase their body temperatures to reach the lower bound of T_{set} .

We used a two-way ANOVA to determine if reproductive groups differed in their effectiveness of thermoregulation and if there was a seasonal component to any difference. We calculated *E* for each individual in each month using the mean monthly d_b of an individual and the mean monthly d_e for that month, and used these values as our response variable. We entered month, reproductive group, and the interaction of these two factors as predictor variables. We conducted the same analysis separately for day (0600–1800) and night (1800–0600). The interaction term was nonsignificant in both cases, and the effect of reproductive group was significant during the day, but not at night (Table 5). Tukey-Kramer hsd tests indicated that during the day, gravid females had significantly higher E values than males and nongravid females, but that males and nongravid females were not significantly different from one another (Fig. 5).

Thermal exploitation

The thermal exploitation index (E_x) , proposed by Christian and Weavers (1996), is the proportion of $T_{\rm b}$ falling within T_{set} when climatic conditions permit. In addition to E_x , we also calculated the proportion of T_b falling below and above T_{set} when T_b values within T_{set} could be achieved. Thus, in calculating these three indices of thermoregulation, we restricted the analysis to times when T_{set} could be reached in at least one habitat (i.e., times when $d_e = 0$ in at least one habitat) and determined the proportion of $T_{\rm b}$ values below, within, and above T_{set} . Over the three active seasons, we collected $T_{\rm e}$ data for 10835 h (i.e., $T_{\rm e}$ data were missing for only 145 h over the three years), and $d_e = 0$ in at least one habitat for 4825 h (44.5% of the time). In total, we obtained 29 722 hourly mean $T_{\rm b}$ measurements from snakes during the active season over the three years, and $d_e = 0$ in at least one habitat for 15189 (51.1%) of these observations. We calculated the three thermal exploitation indices for each individual each year. Averaged across all individuals, the proportion of $T_{\rm b}$ within $T_{\rm set}$ (i.e., $E_{\rm x}$) when it was possible was 22.44 \pm 1.33%. The proportion of $T_{\rm b}$ above $T_{\rm set}$ was 17.22 \pm 1.34%, and the proportion below was $60.34 \pm 2.26\%$.

The index of thermoregulation (E_x) reached its maximum in July (34%) and its lowest point in September (5%) (Fig. 8). July was also the month in which the percentage of T_b values below T_{set} reached a minimum, subsequently increasing to a maximum in September (93%) (Fig. 8). The percentage of T_b above T_{set} was highest in June (25%) and decreased to almost 0% in September. During the course of the day, E_x was at its

TABLE 5. Summary results of the two-way ANOVAs for the effects of month and reproductive group on the index of the effectiveness of thermoregulation (E) of black rat snakes in Ontario for the daytime and nighttime.

Predictor	F	df	Р
Day Month × group Month Group Night Month × group Month	0.733 12.054 3.543 0.471 4.756	8, 322 4, 322 2, 322 8, 322 4, 322	$0.663 \\ < 0.001 \\ 0.030 \\ 0.877 \\ 0.001$
Group	1.004	2, 322	0.369



FIG. 8. Mean percentage of body temperatures (T_b) that fell within the range of preferred body temperatures $(T_{set};$ circles), above the range of preferred body temperatures (upward-pointing triangles), and below the range of preferred body temperatures (downward-pointing triangles) for black rat snakes in Ontario when environmental conditions allowed body temperatures within the range of preferred body temperatures to be reached (A) for each month of the active season and (B) for each hour of the day. Error bars indicate ± 1 sE.

minimum ~0700 and increased gradually to peak ~2200, decreasing thereafter (Fig. 8). During the early morning hours (0300–1000), >70% of $T_{\rm b}$ values fell below $T_{\rm set}$, and $T_{\rm b}$ measurements above $T_{\rm set}$ occurred primarily in the afternoon (1200–1900) (Fig. 8).

We used three two-way ANOVAs to determine whether reproductive groups differed in their thermal exploitation indices ($T_b = T_{set}$, $T_b > T_{set}$, and $T_b < T_{set}$) and whether there was a seasonal component to any difference. We calculated the three thermal exploitation indices for each individual in each month and used these values as our response variable. We entered month, reproductive group, and the interaction of these two factors as predictor variables and conducted the analyses separately for day and night. None of the interaction terms was significant (Table 6), indicating that the relationship between reproductive group and these indices did not vary consistently seasonally. For $T_{\rm h} =$ $T_{\rm set}$, there was no significant difference between groups during the day or at night (Table 6). For the index $T_{\rm b}$ $> T_{\rm set}$, there was a significant difference between groups during the day, but not at night (Table 6). Tukey-Kramer hsd tests indicated that during the day gravid females and males had equal proportions of $T_{\rm b} > T_{\rm set}$, but that both groups had significantly more data points of $T_{\rm b} > T_{\rm set}$ than nongravid females (Fig. 9). Finally, there was a significant difference between the different reproductive groups in the proportion of $T_{\rm b} < T_{\rm set}$ during the day, but not at night (Table 6). Tukey-Kramer hsd tests indicated that during the day gravid females had significantly fewer incidents of $T_{\rm b} < T_{\rm set}$ than nongravid females, but that males were not significantly different from the other two groups (Fig. 9).

Group differences in thermoregulation

One surprising and recurrent result in our analyses of the difference in thermoregulatory behavior $(T_b, E,$ and $E_x)$ between reproductive groups was the lack of a significant interaction between reproductive groups and months. Gravid female black rat snakes only carry their eggs in the early part of the active season (from early June to early July). Therefore, we expected that if there was a difference in thermoregulatory behavior between reproductive groups, this difference should occur during the months prior to egg laying and there should be no difference thereafter, thus producing a significant and consistent reproductive groups \times

TABLE 6. Summary results of the two-way ANOVAs for the effects of month and reproductive group on the indices of thermal exploitation of black rat snakes in Ontario for the daytime and nighttime.

Period	Predictor	F	df	Р
$T_{\rm b} = T_{\rm set}$	$(E_{\rm x})$			
Day	month \times group	1.584	8, 314	0.129
Day	month	23.704	4, 314	< 0.001
Day	group	1.703	2, 314	0.184
Night	month \times group	0.892	8, 119	0.525
Night	month	7.667	4, 119	< 0.001
Night	group	0.361	2, 119	0.698
$T_{\rm b} > T_{\rm set}$	•			
Day	month \times group	1.624	8, 314	0.117
Day	month	32.610	4, 314	< 0.001
Day	group	3.044	2, 314	0.049
Night	month \times group	0.367	8, 119	0.936
Night	month	8.177	4, 119	< 0.001
Night	group	0.411	2, 119	0.664
$T_{\rm b} < T_{\rm set}$	•			
Day	month \times group	0.697	8, 314	0.694
Day	month	51.023	4, 314	< 0.001
Day	group	4.413	2, 314	0.013
Night	month \times group	0.570	8, 119	0.801
Night	month	10.952	4, 119	< 0.001
Night	group	0.680	2, 119	0.509



FIG. 9. Mean percentage of body temperatures ($T_{\rm b} \pm 1$ SE) that fell (A) within the range of preferred body temperatures ($T_{\rm set}$), (B) above the range of preferred body temperatures, and (C) below the range of preferred body temperatures when environmental conditions allowed body temperatures within the range of preferred body temperatures to be reached for the day and night for male (filled bars), nongravid female (hatched bars), and gravid female (open bars) black rat snakes in Ontario. Means with the same letters are deemed not significantly different based on Tukey-Kramer hsd tests.

months interaction. Overall, we found evidence that gravid females thermoregulated more carefully than the other snakes groups (higher T_b , higher E, more incidents of $T_b > T_{set}$ and less $T_b < T_{set}$ when the minimum $d_e = 0$), but no evidence of a reproductive groups \times months interaction. It should be noted that, because T_{set} and T_e s are constant among gravid females, non-gravid

females, and males, the differences we observed in the E index and modified E_x index of gravid females derive from differences in their T_b .

To investigate this absence of a seasonal effect further, we calculated the least-square mean $T_{\rm b}$ (corrected for the effect of mean monthly T_e) and the mean of all four thermoregulatory indices separately for each reproductive group in each month based on mean monthly individual values. Plotting the means as a function of month for each group revealed complex interactions between reproductive groups and months. In all cases, each factor had more than two levels and the differences between the three reproductive groups varied inconsistently in each month (Figs. 10 and 11). This variability and inconsistency in the interactions made them nonsignificant. However, plotting the means as a function of month for each group also revealed that in most cases the difference between gravid females and the other two groups was more pronounced in May and



FIG. 10. (A) Mean body temperatures (T_b) and (B) mean index of thermoregulation effectiveness (*E*) for each month of the active season for male (white circles), nongravid female (gray circles), and gravid female (black circles) black rat snakes in Ontario.



FIG. 11. Mean percentage of body temperatures (T_b) that fell (A) within the range of preferred body temperatures (T_{set}) , (B) above the range of preferred body temperatures, and (C) below the range of preferred body temperatures when environmental conditions allowed body temperatures within the range of preferred body temperatures to be reached for male (white circles), nongravid female (gray circles), and gravid female (black circles) black rat snakes in Ontario.

June, the time that females develop and carry their eggs, than for other months. The mean T_b (adjusted for mean T_c) of gravid females in May and June was $\sim 2^{\circ}$ C higher than the mean T_b of males and nongravid females, whereas it was only $\sim 1^{\circ}$ C higher in July and

 \sim 0.5°C higher in August and September (Fig. 10). Similarly, the mean E of gravid females in May (~ 0.5) and June (~ 0.6) was much higher than the mean E of males and nongravid females in May (~ 0.25) and June (~ 0.3) , whereas the three groups were very similar for the rest of the season (Fig. 10). We observed similar patterns when we considered the thermal exploitation indices. Gravid females tended to have a higher percentage of $T_{\rm b} > T_{\rm set}$ and a lower percentage of $T_{\rm b} <$ $T_{\rm set}$ than males or nongravid females in May and June, but the differences were nonexistent or much less pronounced later in the season (Fig. 11). Therefore, although the reproductive group \times month interactions were nonsignificant in the statistical analyses because of their complexity and inconsistency, it does seem that the thermoregulatory behavior of gravid females differed more from that of the other two groups early in the season (in May and June) when gravid females were developing or carrying eggs.

DISCUSSION

Thermal preference

In the thermal gradient, the upper bound of the preferred body temperature range $(T_{\rm set})$ of black rat snakes (29.8°C) was identical to the upper bound for water snakes from the same location (29.8°C), but the lower bound (26.5°C) and mean body temperature $(T_{\rm b})$ (28.1°C) for rat snakes were higher than the lower bound (24.7°C) and mean $T_{\rm b}$ (27.1°C) of water snakes (Brown and Weatherhead 2000). Lillywhite (1987) reviewed the literature on the preferred body temperature of snakes and summarized the data available for 55 species from five families. Although different methods were used, for the majority of the species mean preferred body temperature ranged from 28° to 34°C and were often close to 30°C (Lillywhite 1987). Thus, black rat snakes seem to have a mean preferred $T_{\rm b}$ at the lower end of the range reported for other snake species. It is possible that species or populations from high latitudes or high altitudes that experience cooler temperatures have lower preferred $T_{\rm b}$ ranges than species that experience more favorable climatic conditions.

General patterns of thermoregulation

Black rat snakes in Ontario rarely exploited their thermal environment to its full extent, at least during the day. Black rat snakes thermoregulated carefully at night (or they simply chose the best thermal habitats when they had no conflicting demands) and were always as warm as their environment allowed from 2300 to 0600. However, when averaged for the whole season, their T_b levels did not attain the lower bound of T_{set} during the day, although T_e indicated that they could have done so for ~10 h/d. Even during the warmest month (July), black rat snakes only maintained T_b within T_{set} for ~7 h/d, whereas T_e indicated that T_b values within T_{set} could have been achieved for 14 h/d. In July, the snakes' slow heating phase lagged by \sim 3.5 h behind the sharp increase in $T_{\rm e}$ values that occurred shortly after sunrise. Body temperature also dropped below the lower bound of T_{set} approximately three hours before $T_{\rm e}$ values did. If the cost-benefit model of thermoregulation applies, these data suggest that for black rat snakes the cost of maintaining $T_{\rm b}$ within $T_{\rm set}$ as long as possible during the day outweighed the benefits of doing so. Brown and Weatherhead (2000) also reported a two to three hour lag time before the morning increase in $T_{\rm b}$ in water snakes, but, contrary to rat snakes, water snakes remained within their preferred range as long as possible in the evening. In fact, water snakes were warmer than the warmest model for most of the evening and night, indicating that they were using some thermal microhabitats that were not sampled by Brown and Weatherhead (2000).

One demand that likely conflicted with thermoregulation in rat snakes was foraging, because rat snakes are active foragers, and time spent thermoregulating cannot be spent hunting. Black rat snakes feed mostly on rodents (Fitch 1963, Stickel et al. 1980). One of the most abundant rodents eaten by rat snakes in our study area is the eastern chipmunk (Tamias striatus), which are abundant in forests (G. Blouin-Demers, unpublished data), the coolest available habitat. Bider (1968) found that chipmunks were most active at dawn and dusk. If black rat snakes hunt chipmunks in early morning and late evening, they would not be able to spend a lot of time thermoregulating at those times, which could explain the delayed heating and early cooling we observed. Other potential factors that could explain the lack of thermoregulation in the morning and evening include predation risk or social behavior. If the predators of rat snakes (e.g., raccoons) are more active at dawn and dusk, or if social behaviors (e.g., mate searching) take precedence over other activities in the early morning, the costs of thermoregulation could outweigh the benefits during those time periods. Evidence consistent with predation risk being higher in the early morning is provided by the fact that snakes were concealed 141 of 180 (78%) times we located them between 0830 and 1000, despite the availability of $T_{\rm e}$ within T_{set} . However, between 1001 and 1730, the snakes were concealed on only 753 of 1128 (67%) occasions we located them.

Effectiveness of thermoregulation

We are aware of only one previous study (Brown and Weatherhead 2000) that has applied the quantitative indices of thermoregulation developed by Hertz et al. (1993) to snakes. Brown and Weatherhead (2000) were also the first to use these indices to compare the thermoregulatory behavior of different segments of a population (i.e., males, nongravid females, and gravid females). Therefore, we can only compare our results from black rat snakes to the results Brown and Weatherhead (2000) obtained for northern water snakes (*Ner*- *odia sipedon sipedon*) studied in the same study area. Although it is not possible to evaluate the extent to which our results are typical of other snakes, together with Brown and Weatherhead's data for northern water snakes, our results for black rat snakes can serve as a basis for comparison for future studies of snake thermoregulation.

The overall index of the effectiveness of thermoregulation (E) for black rat snakes was 0.41, very close to the value of 0.48 reported for water snakes by Brown and Weatherhead (2000). Given the similarity of estimated E for these two species, and the ranges of potential values of E, both might be considered moderately precise thermoregulators. However, as recognized by Hertz et al. (1993), a given value of E can result from a variety of $d_{\rm b}$ and $d_{\rm e}$ combinations, because a ratio enters in the calculation of E (i.e., $d_{\rm b}/d_{\rm e}$). Two species can therefore face different thermal environments and exhibit different thermoregulatory strategies and still have the same value of E if their ratios between $d_{\rm b}$ and $d_{\rm e}$ are the same. Thus, it is also important to consider the magnitude of $d_{\rm b}$ and $d_{\rm e}$ in interpreting E. For black rat snakes, $d_{\rm b}$ was 4.8°C and $d_{\rm e}$ was 8.1°C, whereas for water snakes $d_{\rm b}$ and $d_{\rm e}$ were only 2.4°C and 4.0°C, respectively (Brown and Weatherhead 2000). Thus, water snake body temperatures were, on average, approximately twice as close to their T_{set} as were those of black rat snakes to their T_{set} .

The thermal environment faced by water snakes was also only about half as challenging from a thermoregulation perspective as the thermal environment faced by black rat snakes. Although the general climatic conditions and weather patterns experienced by the two species are the same, black rat snakes are terrestrial and inhabit mostly forested habitats where they receive little direct solar radiation. Those habitats are thus much cooler than the open aquatic habitats inhabited by water snakes. For the three years of this study, $T_{\rm e}$ data indicated that black rat snakes could have achieved $T_{\rm b}$ within $T_{\rm set}$ 44% of the time, whereas water snakes could have done so 53% of the time (Brown and Weatherhead 2000). Therefore, black rat snakes and northern water snakes in eastern Ontario have similar indices of thermoregulation effectiveness (E), but they actually face quite different thermal habitats and experience different $T_{\rm b}$ levels. Evidence that the cost of thermoregulation might be substantially higher for rat snakes than for water snakes in Ontario is provided by the mean $T_{\rm b}$ values, 25% quartiles, and 75% quartiles maintained by the snakes in the field and in the laboratory. Water snakes had almost identical mean $T_{\rm b}$, 25% quartiles, and 75% quartiles in the thermal gradient and in the field when environmental conditions allowed $T_{\rm b}$ to reach within T_{set} . However, rat snakes maintained significantly lower mean $T_{\rm b}$ levels, 25% quartiles, and 75% quartiles in the field than in the thermal gradient.

The effectiveness of thermoregulation index (E) has also been calculated for several lizard species. Hertz et al. (1993) calculated E for six populations of three Anolis species and obtained mean species values ranging from 0.11 to 0.53. Once again, however, we need to consider the magnitude of $d_{\rm b}$ and $d_{\rm e}$ to get a meaningful comparison between these lizard species and black rat snakes. Mean $d_{\rm b}$ varied from 1.1° to 2.5°C whereas mean d_e varied from 2.3° to 4.1°C for the three Anolis species. These deviations are much smaller than the deviations we calculated for black rat snakes. Similarly, mean E calculated for four Varanus species studied by Christian and Weavers (1996) in Australia was ~ 0.5 , but the mean $d_{\rm b} \approx 2.8^{\circ}{\rm C}$ and the mean $d_{\rm e} \approx$ 6.3°C. Thus, although black rat snakes have an overall E similar to the other species that have been studied to date, their $T_{\rm b}$ values were much further from their $T_{\rm set}$, and their environment was more challenging from a thermoregulation perspective relative to the other species.

Thermal exploitation

The thermal exploitation index (E_x) of black rat snakes (22.4%) was only about half the value of E_x of the water snakes (44.4%) studied by Brown and Weatherhead (2000). The E_x of rat snakes is also lower than the E_x that has been calculated for lizards. Christian and Bedford (1995) reported E_x values that ranged 77– 96%, depending on season, for the frillneck lizard (*Chlamydosaurus kingii*) in Australia. The thermal exploitation index varied from 0% to 100%, depending on species and season, and averaged ~46% for the four species of monitor lizards (*Varanus*) studied by Christian and Weavers (1996). Thus, black rat snakes appeared to exploit their thermal environment much less than the single other snake species and the few lizard species for which E_x values are available.

Group differences in thermoregulation

In viviparous snakes, gravid females thermoregulate more carefully than nongravid females and males (Charland and Gregory 1990, Tu and Hutchison 1994, Brown and Weatherhead 2000). This difference in thermoregulatory behavior has also been suggested (but not demonstrated) to cause differences in habitat use, with gravid females preferring habitats that provide the best opportunities for behavioral thermoregulation (Reinert 1993). Blouin-Demers and Weatherhead (2001) showed that gravid female black rat snakes have a stronger preference for edge habitats than nongravid females and males, and here we showed that the thermal quality of habitat edges was higher than other available habitats. Our findings in this oviparous species seem to parallel the patterns that have been documented for viviparous species, and we thus expected to find that gravid female black rat snakes thermoregulated more carefully than nongravid females and males.

The lack of significant differences in T_{set} between the three reproductive groups in the laboratory thermal gradient indicated that females do not alter their preferred

 $T_{\rm b}$ when gravid. However, several lines of evidence suggested that gravid female rat snakes in the field thermoregulated more carefully than other snake groups during the day. (1) Gravid females maintained significantly higher levels of $T_{\rm b}$ than males and nongravid females. (2) Gravid females had significantly higher *E* values than males and nongravid females. (3) Gravid females had significantly more instances of $T_{\rm b}$ that fell above $T_{\rm set}$ and significantly fewer that fell below $T_{\rm set}$ than nongravid females at times when $T_{\rm set}$ could be reached in at least one habitat. To our knowledge, this is the first demonstration that gravid females of oviparous snake species thermoregulate more carefully than nongravid females and males.

Because gravid female black rat snakes only carry their eggs for a relatively short time (nesting occurs during the first two weeks of July), we had anticipated that the difference in thermoregulatory behavior between reproductive groups should be apparent only in the early part of the season when females are actually carrying eggs. We had also anticipated that this difference should be less pronounced than in viviparous species where gravid females carry their offspring for most of the active season, because in oviparous species a large proportion of embryonic development occurs while the eggs incubate in nests. However, we found no significant interactions between reproductive groups and months in our analyses of the effect of these factors on thermoregulatory behavior. The interactions between reproductive groups and months were complex and inconsistent, and therefore nonsignificant. However, we did find that differences in thermoregulatory behavior between gravid females and the other snake groups were more pronounced during May and June when female rat snakes carry their eggs. In the northern water snakes studied by Brown and Weatherhead (2000), the differences in thermoregulation between reproductive females and the other snake groups were most obvious during July and August. Thus, reproduction affects thermoregulation of females in both viviparous and oviparous snake species, and the timing of the change in thermoregulatory behavior coincides with the time that the benefit of maintaining high body temperature is greatest.

Problems with the current indices of thermoregulation

The ratio nature of E presents other problems in addition to the one already discussed, where several species that experience different climatic conditions and have different thermoregulatory behavior have similar values of E. In a statistical sense, ratios are rarely desirable, because they are sensitive to extreme values in the numerator and the denominator (a problem noted by Christian and Weavers [1996]) and their sampling distribution is severely skewed, which creates serious statistical artifacts. For example, if two thermoconformers both have d_p values only 0.1°C lower than the $d_{\rm e}$ of their respective habitat, and one occupies an area that is thermally challenging ($d_e = 10^{\circ}$ C) and the other an area that is benign ($d_e = 0.1^{\circ}$ C), their respective E values will be almost pure thermoconformer (E = 1 -9.9/10 = 0.01) and pure thermoregulator (E = 1 - 0/0.1= 1). Thus, E performs poorly in describing the thermal ecology of species that live in thermally benign habitats such as the tropics, which accounts for the majority of reptile species (Shine and Madsen 1996), because even species that are close to being thermoconformers ($d_{\rm b}$ $\approx d_{e}$) get moderate to high E levels when d_{e} is small. In addition, this index performs poorly at describing the thermal ecology of thermoregulators $(d_{\rm b} \ll d_{\rm e})$ inhabiting challenging habitats, because E remains low to moderate when d_e is large. In summary, E is problematic because (1) it is not defined if the thermal environment is perfect $(d_e = 0)$, (2) it is impossible to interpret without considering the respective magnitudes of $d_{\rm b}$ and $d_{\rm c}$, and (3) it can give spurious representations of the thermal ecology of a species because it uses a ratio. Thus, we recommend abandoning the use of E and propose a simpler index of the effectiveness of thermoregulation defined as the difference between d_{e} and $d_{\rm h}$. This index provides an open-ended scale where negative numbers represent animals that avoid thermally favorable habitats, zero represents perfect thermoconformity, and positive numbers represent animals that thermoregulate to some extent. The magnitude of the difference is a measure of how much an animal departs from thermoconformity, and thus is an index of the effectiveness of thermoregulation.

Christian and Weavers (1996) also proposed alternatives to E. Their thermal exploitation index (E_x) is such an alternative. This index quantifies the extent to which a species exploits its thermal opportunities. In addition to using E_x , Christian and Weavers (1996) also calculated E only for the time periods where $T_{\rm b}$ values within the T_{set} range are available and judged that, under these conditions, E provided an acceptable index of the effectiveness of thermoregulation. However, these two alternatives on their own are also incomplete, because they give no indication on how thermally challenging the environment is or how closely $T_{\rm b}$ measurements match T_{set} when T_{e} values within T_{set} are not available. Thus, to get a complete picture of the thermal ecology of a species, we propose the following: (1) d_e should be used to quantify the thermal quality of the habitat, (2) $d_{\rm b}$ should be used to determine the accuracy of $T_{\rm b}$, (3) $d_{\rm e} - d_{\rm b}$ should be used to quantify the extent of departure from perfect thermoconformity (the effectiveness of thermoregulation), and (4) the modified E_x (Brown and Weatherhead 2000) should be used to determine the extent to which a species exploits the available opportunities for behavioral thermoregulation.

Cost-benefit thermoregulation model

The cost-benefit model of thermoregulation predicts that ectotherms living in habitats where it would be too costly to thermoregulate precisely should be thermoconformers (Huey and Slatkin 1976). Because our study population of black rat snakes is close to the northern limit of snake distributions, we had predicted that their thermoregulation costs should be very high and thus they should be thermoconformers. The environment inhabited by black rat snakes was indeed more challenging from a thermoregulation perspective than the environment inhabited by other reptiles studied so far. However, contrary to our predictions, the calculations of the effectiveness of thermoregulation (E)indicated that black rat snakes were moderate thermoregulators and fell within the same range as other species that inhabit more benign climates. However, given the problems associated with E, we also compared the thermoregulatory behavior of black rat snakes and other species using our alternative index of the effectiveness of thermoregulation: $d_e - d_b$. The index $d_{\rm e} - d_{\rm b}$ was higher for rat snakes (~3.3°C) than for northern water snakes (~1.7°C; Brown and Weatherhead 2000) or Anolis lizards (~1.1°C; Hertz et al. 1993), but approximately the same as for Varanus (~3.5°C; Christian and Weavers 1996). These data indicate that despite the thermal challenges faced by black rat snakes, they depart at least as much from perfect thermoconformity as other species that inhabit more benign thermal environments. Conversely, the thermal exploitation index (E_x) calculated for black rat snakes in Ontario was only about half the $E_{\rm x}$ for other species that inhabit less thermally challenging habitats, indicating that black rat snakes exploited their thermal environment less than these other species. One problem in defining the thermoregulatory strategy of an ectotherm is that a strategy cannot be defined by a single parameter, but actually requires a set of different parameters (Hertz et al. 1993). Thus, whether or not our results for black rat snakes support the current costbenefit model of thermoregulation depends on which parameters we use to define their thermoregulatory strategy. Based on their effectiveness of thermoregulation $(d_{\rm e} - d_{\rm b})$, rat snakes seem to be at the upper end of the continuum of thermoregulatory strategies, despite their very challenging thermal environment, hence the cost-benefit model would not be supported. Conversely, based on their thermal exploitation (E_x) , they are closer to being thermoconformers and thus would support the current model. Unfortunately, our data on black rat snakes can only be compared to data for other species in other areas. A problem in drawing inferences from interspecific comparisons is that one must assume the species being compared only differ in the variable of interest, which is unlikely to be true. Therefore, strong tests of the cost-benefit model will require data for the same species in habitats varying markedly in thermal quality. Awaiting such data, we can only reach preliminary conclusions regarding the broad applicability of the cost-benefit model of thermoregulation.

Shine and Madsen (1996) have argued that thermoconformity may be widespread in species that live in tropical areas, where $T_{\rm e}$ values in the range of $T_{\rm set}$ are always available at a low thermoregulatory cost. Snakes in those areas are thermoconformers, despite experiencing very small variations in $T_{\rm h}$ (stenothermy). A likely explanation for this pattern is that the physiological costs of thermoconformity are very low when the thermal environment is benign, because even without thermoregulation, $T_{\rm b}$ is close to $T_{\rm set}$. Although the cost-benefit model of thermoregulation (Huey and Slatkin 1976) recognized that the advantages of thermoregulation decrease in low-cost habitats (hence one can infer that the cost of thermoconformity also decreases in these habitats and increases as the thermal quality of the habitat decreases), the model puts more emphasis on the premise that the cost of thermoregulation increases as the thermal quality of the habitats decreases. However, the cost of thermoconformity might be more important than heretofore recognized, and might force species in more challenging habitats to thermoregulate more carefully.

Brown and Weatherhead (2000) hypothesized that the consequence of living at high latitudes for snakes may be a short active season, but that activity within this active season may not be restricted because the water snakes they studied faced a benign thermal environment during the active season. The shallow marshes inhabited by water snakes offered almost continuous access to $T_{\rm b}$ values within $T_{\rm set}$ for most of the active season (Brown and Weatherhead 2000). Similarly, we demonstrated that the active season of black rat snakes within the same study area was very short (~5 mo). In the case of black rat snakes, however, $T_{\rm e}$ was within T_{set} on average 11 h/d in the habitats that received direct solar radiation. In the habitats that did not receive direct solar radiation, mean $T_{\rm e}$ was never within T_{set} . Such habitats included forests, the most common habitat in the study area (Blouin-Demers and Weatherhead 2001). Therefore, although black rat snakes had access to all habitats, their activity was thermally constrained (at least to some extent) in all habitats and very constrained in the most common habitat. This situation contrasts with the largely thermally unconstrained activity of the water snakes studied by Brown and Weatherhead (2000). Thus, it does appear that, at least for some snake species, high latitudes constrain both the length of the active season and activity within the active season.

ACKNOWLEDGMENTS

Our experimental procedures were approved by the Carleton University Animal Care Committee (Protocol B97-1). We thank E. O'Grady, H. McCracken, A. Moenting, J. Svec, and T. Volk for their help in data collection. We are particularly indebted to C. Verreault for her gratuitous help with many aspects of this study. Several people contributed very helpful discussions that improved this work. We are especially grateful to G. Brown, K. Dufour, K. Kissner, C. Parent, K. Prior, and S. Sommerer in this regard. C. Shilton was very patient in training one of us (G. Blouin-Demers) to perform surgical implantation of radio transmitters. We are also grateful to the Queen's University Biological Station for logistical support. Funding for this research was provided by Parks Canada, World Wildlife Fund Canada, a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to P. Weatherhead, and NSERC postgraduate scholarships to G. Blouin-Demers.

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